THE DISTRIBUTION OF *COLIAS* IN THE EQUATORIAL ANDES (1)

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The Genus *Colias* of primarily yellow and orange Pierid butterflies, is largerly northern in distribution. Representatives are found from Europe across the great Eurasiatic land mass to Siberia and northern Japan from where they span the narrow water barrier separating America and occur throughout North America. In the Mediterranean region, representatives are found on both the European and the African shores of the sea and also are found south around the Sahara desert through the highlands of Ethiopia and the Sudan into the southern parts of that continent, being absent in the hotter and more humid places.

Representatives are found at various elevations in the Himalayan mountain mass but shun the hot and humid plains of India to the south. No Colias is known throughout the hotter southeastern territory of Asia, nor in the islands of the Indian and Pacific Oceans, nor in Australia, New Zeeland or Tasmania.

In the Americas, Coliads are distributed from as close to the North Pole as there is land (Northern Greenland at 82° North Latitude) to the southern portion of the Mexican plateau without a break in the continuous distributional range. Separated by the tropical isthmus of Tehuantepec from the Mexican plateau a colony exists in the highlands of Guatemala. Apparently, no Colias is able to withstand the hot, humid conditions of the tropics and, except for transitory populations, these are absent in such portions of the southeastern United States, Central America, the islands of the Caribbean Sea and South America that have such a climate.

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1. Since *Trifolium repens* is at the present time the primary food plant of *Colias dimera*, the general distribution of the European plant is given too.
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The Cordillera of the Andes, the high mountain mass extending from 55° South Latitude to 10° North Latitude, has provided the cooler conditions necessary for the life of Colias in an area otherwise expected to be devoid of these forms of life. From some unknown point in Venezuela, several species of this genus are distributed along the length of this mountain chain to the cooler portions in the south of Argentina and Chile where climates are suitable at sea level. In the latter area, one species, *lesbia,* has become an agricultural pest on the forage plant, alfalfa, grown by man in large quantities.

The Andean mountain chain gives the appearance of a single, narrow, high mountain mass extending from Patagonia to Bolivia in an almost straight south to north line. In Bolivia and southern Perú there is a widening out in the vicinity of an elbow joint at Lake Titicaca. North of this point the chain is narrow again and extends in a more westerly direction towards Ecuador. With Mt. Chimborazo as a pivot point, the chain turns eastwards once again to just north of the equator, at which place there is a great widening-out process, the result of which is the formation of two rifts in the cordillera forming the valleys of the Cauca and the Magdalena rivers. On either side of these rifts, the new cordilleras fan out; the *Cordillera Occidental* curves to the west and continues in connection with the cordillera in Panamá and Central America; the *Cordillera Oriental* curves to the east and ends at right angles to the original range at Trinidad where connection is made with the Antillean islands mountain chain; the *Cordillera Central* between the two rifts proceeds in a northern direction until its culmination at the junction of the Cauca and Magdalena Valleys.

Now, the Andes until its splitting into three parts, have had a central section rather wide and at high elevation, giving to considerable area a temperature or cool climate in an equatorial region. The result of this is terms of primitive human populations was the development of the Inca empire which existed north only to the splitting of the mountain mass. In butterfly distribution too, some cold climate species reach their northern limits at this point.

North of the area of the Andean split extensive areas suitable for the development of the latter cold climate species are much scarcer. The *Cordillera Occidental* has almost none at all; there are only small mountain ridges available and these in the form of islands. The *Cordillera Central* is high in elevation (above the snow line in some places) but the elevation drops off rather suddenly to the warm or hot valley floors of the Cauca and Magdalena so that little except mountain slopes is left for the cold areas. The *Cordillera Oriental* is relatively low and has but little high, cold territory from the southern connection with the main range until the savanna of Bogotá. From this point north to Chiquinquirá, Tunja and Sogamoso, there is again extensive cold plateaux. In the Sierra Nevada del Cocuy, small high valleys continue this plateau area into the Cordillera de Mérida in Venezuela.

Colias Ecological Preference in this Region

The conditions under which Colias will live are of two limiting classes, namely (1) the conditions which are favorable for its very specific food plants and (2) the conditions necessary for its own development in addition to that of its host.

Considering now only *Colias dimera* of this region and the distribution of its larval food plants, it is found that these (*Trifolium repens* and *T. dubium*) are limited in all regions personally visited in between the elevations 2000 meters and 3500 meters above the level of the sea but being primarily abundant in wet places in a narrow belt only between 2500 meters and 3000 meters. This is only 500 meters in vertical distribution. The extent of such areas in the Andean cordilleras are largely as given in the preceding paragraph. The map (fig. 1) outlines the territory above approximately 2500 meters.

It has been found that, except for one case, wherever the wild conditions are suitable for the food plants they are also suitable for this Colias. Transplantation of these Trifoliums down to an elevation of 500 meters above the level of the sea has been found satisfactory for the production of vegetation but no attempt to flower has been noticed beyond those produced at the place of origin. However, the plants must be kept in isolation, well screened, as protection against several noctuid moths which seem greatly to outgrow the plants. At the cooler temperature above 2000 meters apparently the plant is largely able to outgrow the larvae since both are present. Colias at 500 meters elevation have been found to grow well from the egg stage with protection against various insect predators but the adults so grown are found to be sterile (at temperatures, maximum 32º C. day and minimum of 24º night).

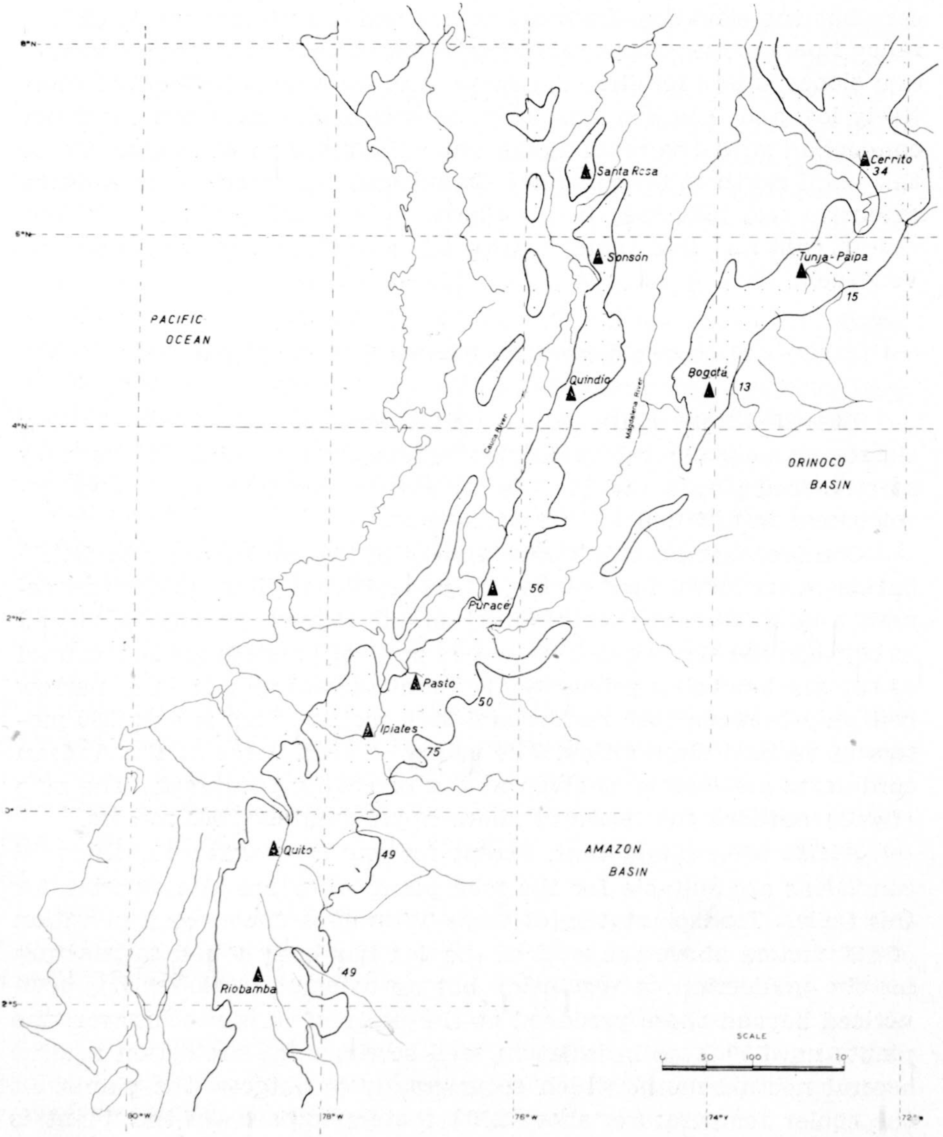
8°N
6°N
4°N
2°N
0°
2°S
80°W
78°W
76°W
74°W
72°W
PACIFIC OCEAN
Santa Rosa
Cerrito
34
Sonsón
Tunja-Paipa
15
Quindio
Bogotá
13
Cauca River
Magdalena River
ORINOCO BASIN
Puracé
56
Pasto
50
Ipiates
75
Quito
49
AMAZON BASIN
Riobamba
49
SCALE
0
50
100
200

Fig. 1.—Map illustrating the distribution of Colias in the equatorial Andes of Colombia and northern Ecuador The dotted area represents Andean terrain above about 2600 meters in elevation and which is largely suitable for *Colias dimera*. The localities sampled for gene frequency are marked, and the whole numbers shown are the white female frequency in *Colias dimera*.

Colias Distribution as Observed in the Field

The actual range of conditions under which *Colias dimera* has been seen in the wild includes up to 4000 meters in elevation in the Sierra Nevada del Cocuy. These individuals were certainly not resident and were flying very fast. The low elevation of 2000 meters has been observed in several places.

The region of Cerrito: Cerrito is a small village in the valley of the Rio Servitá on the northwestern side of the Sierra Nevada del Cocuy (fig. 1). At this point, the *Cordillera Oriental* divides into two parts on either side of Lake Maracaibo. North of Cerrito there is high, cold terrain only to about Mérida in Venezuela so that this may be the limit of Colias range. Southwards, the area is in continuous connection with Colias populations to Bogotá, through partly isolated by the valley of the Chicamocha. In the valley of the Servitá, Colias were first seen at 4000 meters but were very rare at 3000 meters. Clover was almost absent above 3000 meters and none was observed in the bogs of Almorzadero at near 4000 meters. At about 3000 meters and down to 2200 meters (at Málaga), there were many meadows mostly extended in size by irrigation flooding on the hill slopes in which Colias were abundant. Despite the abundance of white clover in the pastures just above Málaga (2200 meters), Colias were not so abundant here as higher up between Concepción and Cerrito at 2500-2600 meters. Much above 2800 meters here, meadows were rare and not much clover was observed. These clovers prefer wet places in meadows. Below Málaga, no clover nor Colias were observed at all.

On the south side of the Chicamocha valley, the same sequence of events was observed. The lower portions of the valley (*canyon* in the North American sense) are desert, with giant cacti and foliage-reduced plants predominating. Up to 2000 meters no Colias were observed in the meadows produced by irrigation. However they were very abundant in the many meadows near Susacón (2500 meters). Likewise Trifolium was very abundant. In the high páramo between Susacón and Duitama no Colias were observed above 3000 meters. Continually, however, on the plateau to the south (2600 meters) these were abundant.

The Paipa-Tunja area: From Tunja and north to Sogamoso, the Río Chicamocha drains a high valley of 2500-2700 meters in elevation which is surrounded by a brushland of near páramo. The samples were obtained at several points from Tunja to Paipa but primarily at one midway point. Colias were present nearly everywhere but always commonest in the wettest places.

The Bogotá area: Trifolium and Colias are both exceedingly common on the Bogotá savanna at an elevation of 2600 meters (Facatativá, Sibaté, Fontibón, Salto de Tequendama, Soacha, Techo, Bogotá, Chapinero, Chía, Usme, etc.). Where there is sufficient water for Trifolium along stream beds up to at least 3500 meters these also occur but are of course not so abundant as on the savanna where conditions are more favorable. In the canyon of the Bogotá river immediately below the falls of Tequendama (at 2400 meters), both Trifolium and Colias have become scarce and are completely absent below at about 2200 meters. This is likewise true for the same elevations just below San Miguel on the canyon leading to Fusagasugá. Along the railroad leading from Facatativá to the Magdalena Valley at Puerto Salgar, clover and Colias seemed very abundant at about 2400 meters but here there was available a greater area of meadow lands for their development.

The same conditions are true for the eastern slopes of the *Cordillera Oriental*. Both Trifolium and Colias are found in wet places from the top of the pass at the páramo of Cruz Verde down to Chipaque at an elevation of 2400 meters. Colias are rarely seen below Chipaque so it seems that the altitudinal preferences are the same on both sides of the cordillera.

The Eastern Cordillera south of Bogotá: From the plateau of Bogotá south to its junction with the central cordillera, the eastern range is mainly a ridge or series of ridges. At two points as shown on the map the range is broken by depressions lower than 2000 meters so that the Bogotá zone is isolated from that to the south. This, of course, effectively separates the *Colias dimera* populations on the two sides of the Magdalena river and prevents gene interchange.

The Santa Rosa area: At the most northern end of the central Cordillera, a portion of the mountains is split into two parts by the Rio Nechí or Porce, cutting the main range at a tangent. At about the place where this split begins (near Medellín) the connection between the western section and the main mass is below the Trifolium zone. This fact combined with aridity in the area seems to isolate the northern section at an elevation high enough to support Trifolium.

White clover was first observed on the road from Medellín at about 2300 meters elevation in isolated wet places. It occurs in such small draws or along creeks and springs up to about 2700 meters or more where such places exist. The vicinity of Santa Rosa is hilly and would be suitable for clover pastures if it had enough water. The latter is not available for irrigation owing to the lack of higher mountains nearby. The two species of clover were in this vicinity as at Tunja but Colias were without doubt completely absent. The lack of Colias is probably due to the relative scarcity of the food plants combined with the isolation from the main Colias populations in the central and eastern cordillera, despite the great expanse of territory at suitable elevations.

The Sonsón area: The area just south of Medellín and the Rio Porce has the most northern population of *Colias dimera* in the central cordillera. White clover was first observed in this area in the canyon just above Medellín at less than 2000 meters but it was not common. The ridge of the mountain here (at 2500 meters) had considerable clover but there was little space available not covered by chaparral. Only the ridges in this vicinity are high enough for it but between La Ceja and La Unión, the ridge has sufficient area and water and it was here that *Colias dimera* was first observed. It exists certainly all along the ridge but was not observed again on the road until near Sonsón where meadows were again present at elevations over 2500 meters. The main valley near Sonsón is at only 2300 meters elevation but the meadows are continuous with the town at 2500 meters on the mountain slope. Apparently the higher slopes are too dry and the valley floor too warm for the existence of much clover since the latter was relatively scarce. Of the day's observation in excellent weather, there were observed only 15-20 males and 8 females over a distance in extent of many kilometers. The presence of the tropical meadow species *Anatia jatrophae* and *Therias limbia* indicates that the place is too warm for Colias to exist comfortably (Hovanitz, 1944d). At no other known locality were these tropical zone indicators encountered in company with Colias.

The Puracé-Sonsón area: It would have been desirable to have had for comparison samples from the central cordillera north of Puracé, especially at a place of the same latitude as Bogotá (Quindío). However, it does not seem likely that any place exists where a sample could be obtained easily. Observation of the Sierra in the area of Manizales (Páramo del Ruiz) and Armenia (Páramo del Quindío as shown on the map) indicates that the range is too precipitous for much meadow land above 2500 meters, the land being occupied by chapparral of brushland. These places are on the north and south sides of the Sierra Nevada del Ruiz and Tolima, the highest parts of the central cordillera. Apparently from Sonsón south there is continuous páramo along the ridge to Puracé. On either side of this ridge there should exist places, however small, that could support small numbers of *Colias dimera*. White clover was observed at both the above mentioned places but Colias was observed only at Quindío, though not in sufficient quantity for a sample.

The Puracé area: Puracé is located on the western side of the *Cordillera Central* of Colombia directly above Popayán at an elevation of 2,780 meters. This point in the cordillera is just north of the place where the *Cordillera Oriental* branches from the main Andean chain and is on the steep slopes of the volcano Puracé.

In Ecuador, despite the recognized existence of only one chain of peaks and volcanoes, these are so arranged that they superficially form two recognizable ranges. These are called the *Cordillera Oriental* and the *Cordillera Occidental*. Between the ranges, however, unlike in Colombia, the valleys are very high, forming the high Andean valleys or plateau. Watershed dainage between these ranges is parallel with the cordillera for only short distances, the rivers then cut through the ranges and go at right angles to the sea. Just north of Pasto, this central "plateau" between the ranges drops in elevation to form the small valley of the Patía and then the long valley of the Cauca. North of Popayán (near Puracé) the drainage is only north into the Caribbean sea. The western cordillera of Ecuador becomes continuous with that of the same name in Colombia while the eastern cordillera of Ecuador becomes the central of Colombia, which a little farther north gives off the eastern of Colombia.

Puracé then is the most southerly locality of which we have records before the region of the combined Andean uplands is encountered at Pasto.

In the canyon leading up to Puracé from Popayán some white clover was noticed at an elevation of 2000 meters; also a few Colias. The clover was growing along the streams here and up to 2500 meters. At this higher elevation it seems to scatter more in the meadows but is restricted only to very wet places and places where the soil is relatively undisturbed by farming, such as the village cemetery. Colias and clover were observed up to more than 3000 meters in this region but the upper limit is not known. Puracé itself is considered as at about the population center since clover is most widely spread in the area.

The Pasto area: Pasto is at the most northern point where the Cauca trough reaches an elevation suitable for Colias. Pasto is situated in a valley surrounded by meadows much higher than itself. The low elevation given for the town is thus misleading for the Colias population in the vicinity. Here *Colias dimera* have been seen everywhere from 2500 to 3000 meters; other elevations have not been examined. White clover is exceedingly common in all wet places, irrigated hill slopes and bottom lands.

The Ipiales area: Ipiales is 2,910 meters in elevation and is on one side of a very high table-land covered by meadows averaging 2900 meters. Túquerres (3100 meters) and Tulcán (3100 meters) are other towns on this same tableland. The region is partly isolated from the north by the canyon of a branch of the Río Patía and on the south by the canyon of the Río Chota or Mira. All this tableland is abundantly covered with the two clovers used by *Colias dimera*. No attempt was made here to see how much higher or lower than this tableland Colias extended. An aerial view of the terrain indicates that meadows do not exist much above 3000 meters. The hill tops are largely covered with a chaparral and the lower and steeper canyon slopes also by brush. Therefore, the elevations given are considered as the population center for Colias in this area.

The Quito area: Quito is located on a narrow but low valley averaging about 2,800 meters in height. To the west are the mountain peaks culminating in Pichincha (4,787 meters) with meadows at least to 3500 meters. To the east, over a low range of hills, is the valley of the Rio San Pedro at about 500 meters lower in elevation though rising to join the valley of Quito to the south. Meadows are however absent here in the lower parts because of the great aridity of the low interandine valleys such as this.

To the south, the meadows of the Quito region rise to the Pass of the Volcano Cotopaxi (3500 meters). To the north, they disappear in the canyon of the Rio Guaillabamba which cuts across the range after draining the interandine tablelands. Clover meadows extend therefore up to 3000 meters and down to about 2500 meters, being most abundant at about 2700-2800 meters at Quito. Meadows at the Pass of

Cotopaxi at 3500 meters and down to 3000 meters are too high for much clover or much *Colias dimera*. This would indicate that the Ipiales area is at about the maximum.

The Riobamba area: At 2,750 meters, Riobamba is in a valley watered primarily by irrigation, surrounded on all sides by high mountains of which Chimborazo (6,310 meters) is the highest. Trifolium and Colias population are separated from those of Quito by the páramo of Chimborazo (3900 meters) with no Colias nor clover, the interandine valley of Latacumba or Ambato and then the páramo of Cotopaxi (3500 meters).

Colias populations are very abundant between 2600-2800 meters but meadows here are commonest at 2800 meters. In this region, valleys below about 2600 meters are transformed into steep canyons which are not favorable for the develppment of meadows and except for the irrigated flat lands, the upper portions are very dry owing as much to the character of the porous, volcanic-dust soil as to the sparsity of the rainfall. As in the Pass of Cotopaxi, no Colias were observed abundantly in the pass of Chimborazo above 3200-3500 meters.

Factors entering into the Distribution of the White Female Frequencies.

In the Northern Hemisphere, it was observed that the white female form was commoner in the north than in the south in the two semi-independent races of *Colias chrysotheme* (Hovanitz, 1944a), In another major group in North America, this is likewise the case (*Colias occidentalis, harfordii, alexandra,* etc. complex). In many Colias species that exist only in the very far north, the almost abundant female form is the white. This seems to be true in reverse for the southern parts of South America as well. Those forms that occur in Patagonia and Tierra del Fuego seem to have mainly white females there (*vautieri, lesbia*). In view of this correlation of *increase in the white female frequency with increase in latitude* it was interesting to investigate populations of Colias in the vicinity of the equator.

One might expect that the white frequency would be exceedingly low in the vicinity of the equator. However, very different conditions prevailing between the Tropics of Capricorn and Cancer have given a very different result. In this zone or band around the world, there is no special season during the year that is especially hotter or colder than another. With the exception of a slight difference due to wet or dry season, temperature variations are altitudinal rather than latitudinal (1° C. corresponds roughly to 170 meters of altitude). Therefore, for the most part the climate in any one place has about the same temperature all the year round and the primary fluctuations are daily.

For the growing insect, these differences between the equatorial and temperate climates are fundamental. Any insect must be able to withstand the entire fluctuation of climatic conditions during its entire life cycle in the equatorial regions, rather than, as in the polar regions, just a part of it. A Colias butterfly in the northern hemisphere, for example, can go into diapause and withstand freezing temperatures for six months of the year as a larva and then during the other six months enjoy warm weather for its full development and sexual activities. Any stage of the insect other than that in diapause is likely to be killed by the freezing conditions of the winter. On the other hand, for some insects the winter season may be favorable for life but the summer season too hot for full adult development (*Colias chrysotheme* in the southern portions of its ranges). North or south of the Tropics of Cancer or Capricorn, then, life may be conditioned by either the maximum of minimum climatic factor (primarily temperature) upon a particularly sensitive period of the development. By correlation of the life stages with the alteration of the season, the insects are able to withstand otherwise unfavorable conditions.

Such correlation is practically impossible in the equatorial regions as the seasonal differences are so slight. Any stage in the life cycle, egg, larva, pupa or adult must withstand all conditions in the territory in which it lives. The insect is subjected daily to maxima and minima. Yet such conditions as maxima and minima are not effective as such without knowledge of lethal dosage, the length of time of exposure before such conditions are effective. For example, *Colias eurytheme* is rendered sterile if grown continously at a temperature much above 26º C. with a high humidity. But it can exist and find nearly optimum conditions in an environment with daily temperature rising to more than 40º C. in alternation with less than 25º C. It can withstand freezing temperatures without diapause for several hours but would die if this were continued.

A Colias at an elevation of 2,800 meters at Quito has a median average temperature of 13º C. But the daily fluctuation may be as much as 26.5º C. maximum to 3.6º C. minimum. At a nearby place, Cotopaxi (3,590 meters), the average temperature is 7.1º C. with recorded maximum and minimum of 18.4º C. and -0.2º C. respectively. Any stage of *Colias dimera* or Trifolium must be able to live at near freezing, therefore.

The Geographical Differences in the White Female Frequency.

In table 1 are shown some of the factors entering into a consideration of the factors influencing the variation in the white female frequency of Colias in the vicinity of the equator from a point nearly 7º North latitude a point nearly 2º South latitude.

First, it is noted that the white females frequencies are not particularly low considering the "equatorial climate" but the temperatures indicates that a low frequency should not be expected.

Secondly, an excellent correlation is obtained between the frequency of the white female in a given region and the elevation or median temperature of that region. It is expected that between the

Table 1.—The frequency in percent of white females as compared with the normal orange females in equatorial populations of *Colias dimera*. Mean temperatures are given for three localities; elevations are "population centers".

Locality	Meters altitude	geographical position	orange ♀	white ♀	Total	%white ♀♀
Cerrito, Colombia..........	2,700	6° 50′ North	158	82	240	34.2
Santa Rosa, Colombia....	2,600	6° 50′ North	—	—	—	——
Sonsón, Colombia.........	2 500	5° 43′ North	7	1	8	——
Tunja-Paipa, Colombia....	2,600	5° 40′ North	321	56	377	14.9
Bogotá, Colombia (15° C)	2,600	4° 36′ North	317	46	363	12.7
Puracé, Colombia.........	2,800	2° 25′ North	46	59	105	56.2
Pasto, Colombia...........	2,700	1° 14′ North	73	76	149	50.4
Ipiales, Colombia (12° C)	2,950	0° 50′ North	52	156	208	75.0
Quito, Ecuador (13° C)...	2 800	0° 14′ South	141	133	274	48.5
Riobamba, Ecuador........	2,800	1° 40′ South	112	109	221	49.3

livable range of 2,500 to 3,000 meters altitude above the sea if the bulk of the population is breeding at 2,500 meters such a population should have the lowest frequency of white females, and conversely if the bulk of a population is breeding at 3000 meters such a population should have the highest frequency. This correlation of *increase in altitude with increase in the white female frequency is well shown in the data.* (fig. 2).

The Distribution by Space

The map (fig. 1) shows the existence of four zones of gene frequency differences. The first is that of Cerrito or the Sierra Nevada del Cocuy where the frequency is 34%. Connected with the Paipa-Tunja areas of half the frequency, it can retain its difference only by selection of the white individuals by some environmental factor. Present in this area and absent elsewhere in the eastern cordillera is the snowy mountain mass above the meadows which accounts for extremely cold nights in the canyons.

The second area is that of Tunja-Paipa to Bogotá with a frequency of 12-15%. Here nearly the entire population is at a near minimum in elevation and has a near minimum in white gene frequency.

The third area is that of Puracé to Riobamba excluding the high points near Ipiales. Here the valleys are intermediate in elevation and the endemic populations of *Colias dimera* have an intermediate white frequency of near 50%.

The fourth area is that of Ipiales where a maximum in elevation (2900-3000 meters) has been accompanied by near maximum in white female frequency (75%).

It seems that the isolation existing between the central and eastern cordilleras of Colombia has been influencial, nevertheless, in the production of two major zones of different gene frequencies, perhaps aiding in the differenciation promoted by the climatic differences.

The Similar Variation in Colias cunninghami (3)

In the localities Pasto, Ipiales, Quito and Riobamba there were observed more or less in the same vicinity of the *Colias dimera* popu-

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3. The authorities for names of butterflies used in the paper are the various authors in the work of Seitz (1924). *Colias cunninghami* according to this work was at that time known only in the male sex and from Ecuador. The existence of females in both white and orange forms may then be first recorded here. Also, the presence of the species in Colombia is probably first recorded here.

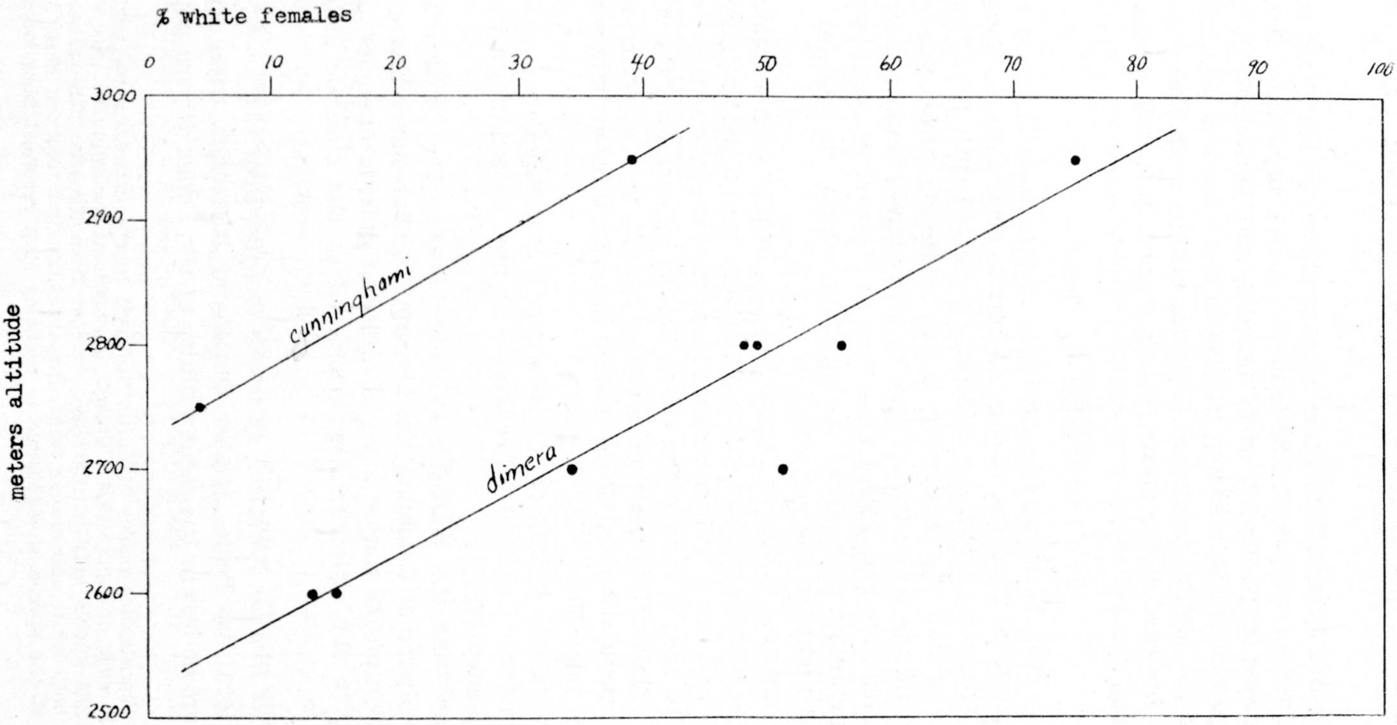

Fig. 2.—The correlation between elevation and the frequency of white females in populations of Colias in the equatorial Andes. Each dot represents a distinct and separated population region except that for *cunninghami* at 2750 meters which includes three similar localities. The correlation between the two Colias is clear, as is the higher frequency or *dimera* at a given elevation and the absence of any *cunninghami* at the lower elevations.

lations individuals of *Colias cunninghami*. This species apparently exists no farther north than Pasto but if the present guess is correct and *cunninghami* is conspecific with *vautieri*, then the southern distribution extends to Tierra del Fuego. By correlation of the *cunninghami* type with similar types in North America, *cunninghami* would be considered an inhabitant of colder country than *dimera*. And this is apparently the case according to the present known distributional range.

A partial ecological isolation exists between the two species of Colias, possibly based upon the respective food plants. The Trifolium which are the food of *Colias dimera* larvae live primarily in the wetter, or lower, portions of meadows. The *dimera* adults, especially the egg-laying females, are likewise most abundant in these places. *Colias cunninghami* is found most abuntantly in higher and dryer pastures; its food plant is however quite unknown. At the higher and colder locality Ipiales, where *cunninghami* was especially common, these differences were seen very strikingly. Here the two species were very common and observation could be made of behavior reactions when in contact. That is, it was desirable to know if any attempt was made at interspecific copulation such as exists between the two races or species of *Colias chrysotheme* in North America (Hovanitz, 1943). The results are negative. No individuals show any sign of actual copulation and no sign of intermediate products was observed. Interspecific attempts to pair were fairly common and were reciprocal but the sexual maneuvers did not last long and were not completed.

As in *Colias dimera* a correlation apparently exists between the locality of the *cunninghami* population and the white gene frequency. The localities seem to have the same effect on *cunninghami* as they did on *dimera*, as Ipiales has a higher frequency than Pasto, Quito or Riobamba (Table 2). It is apparent that though the frequency of the white female form varies in unison in the two species, it is always lower in *cunninghami*, the more cold-loving form (Fig. 2). This same correlation was noticed in the two races of *Colias chrysotheme* in North America.

It was determined that in the two major races or partially sterile forms of *Colias chrysotheme* in North America that the white female controlling gene is fundamentally identical even though it was impossible in this case to determine its identity as far as the chromosome loce were concerned (Hovanitz, 1944b). Now, the fact that in all

Table 2.—Comparison of the frequencies of the white female in *Colias dimera* and *Colias cunninghami* at two different elevations.

Locality	Meters altitude	number white ♀♀	Total ♀♀	% white ♀♀
Ipiales (*dimera*)	2,950	156	208	75.0
Ipiales (*cunninghami*)	2,950	14	36	38.9
Pasto, Quito and Riobamba (*dimera*)	2,750	318	644	49.3

known species of Colias, white female forms react the same way toward similar climatic conditions, in the equatorial regions or in the higher latitudes, suggests certainly that the physiological effect of the gene is the same in all species. Since the climatic conditions preferred by any two species of Colias are apparently always different as shown by their different distributions, it is expected that the advantage conferred by the white female gene would be different in any place where more than one species is able to exist (Fig. 2). That is, the different species possess different reaction norms which are brought into similar reaction toward a given environment by the different white gene frequency.

Relation of these Colias to the Distribution of Alfalfa.

Several species of Colias have apparently developed a preference to alfalfa as larval food (Hovanitz, 1944c). In the paper just cited, it was suggested that *Colias dimera* in Colombia might become a pest of alfalfa if the plant were grown to any considerable extent in this region. With the exception of several scattered fields, this crop does not seem to be very abundant. However, the case is different in Ecuador. Here, alfalfa is very abundantly grown as a forage and hay crop at least between Quito and Riobamba at elevations from 2500 meters to 3000 meters. These are grown usually quite separately from alternating fields of white clover though sometimes they are mixed. The conditions are therefore favorable as a natural test of the desirability of this crop as food for the Colias. The extreme abundance of Colias in clover pastures and their extreme scarcity in the adjacent alfalfa fields is sufficient evidence to indicate that alfalfa at the present time is unfavorable in this region. *Colias dimera* errs however in laying its eggs when alfalfa is close at hand. Several eggs have been found on isolated alfalfa plants in a pasture of clover and in one case a female was observed to be depositing eggs upon one. No females were seen to stop in pure alfalfa fields for the purpose of laying eggs though innumerable examples were observed of the females laying upon the two clovers.

No plants of red clover were observed in Ecuador. However, there were scattered plants on the savanna of Bogotá and toward Tunja and Paipa. Females were observed laying eggs and eggs were observed on these plants. This however is little indication that red clover can be considered a favorable food plant for the species.

Cases of this sort in which the female errs in laying its eggs have been noted many times in the literature and is apparently a common habit in some species. In the evolution of new forms such errors are very important because if a form arose by mutation in which such a new food were satisfactory, it is clear that this would constitute one of the first and major forms of isolation upon which evolution itself depends.

SUMMARY AND CONCLUSIONS

1.—The altitudinal, ecological and latitudinal distributions in the vicinity of the equator of butterflies of the genus *Colias* have been described, together with a study of the frequencies of a genetically-determined white female form in these populations.

2.—Populations of *Colias dimera* were found as far north as the Sierra Nevada del Cocuy near the Colombo-Venezuelan border (6° 50′ North) and as far south as Riobamba (1° 40′ South) in central Ecuador. The range is probably greater than this in both directions.

3.—Populations of *Colias cunninghami* were found as far north as Pasto in southern Colombia (1° 14′ North) and as far south as Riobamba in central Ecuador (1° 40′ South). It is almost certainly determined that Pasto represents the most northward population of this species but its southern limit is unknown (possibly Tierra del Fuego).

4.—The altitudinal distribution of *Colias dimera* is closely correlated with that of the abundance of two species of clovers, *Trifolium repens* and *dubium*. This range is largely between the elevations of 2500 to 3000 meters above the level of the sea, especially where there are present lands level or semi-level and with considerable water.

5.—The altitudinal distribution of *Colias cunninghami* is at elevations similar to *dimera* but apparently preferring slightly higher regions. Ecologically it prefers open pasture land which is not as wet as that preferred by *dimera*. The food plant of the larvae is unknown.

6.—Alfalfa (*Medicago sativum*) is apparently largely ignored by both species of Colias where abundant fields of it occur in Ecuador.

7.—The white female frequency in the Colias species is shown to vary with the altitude of the population. This corresponds in non-tropical regions with latitudinal changes with regard to average temperatures. Higher altitudes or higher latitudes = higher white female frequency. Lower altitudes or lower latitudes = lower white female frequency.

8.—The two species of Colias vary in unison in their geographical ranges in the equatorial region just as other Colias do at the higher latitudes. The more cold-loving species always has the lower frequency of the white female at a given place that the other. It seems reasonable to conclude, therefore, that the physiological effect of the gene responsible for the white female is the same, essentially, in all species.

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